Convergent evolution, superefficient teams and tempo in Old and New World army ants

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Swarm raiding army ants, with hundreds of thousands or millions of workers per colony, have evolved convergently in the Old World and New World tropics. Here we demonstrate for the first time, to our knowledge, superefficient foraging teams in Old World army ants and we compare them quantitatively with such teams in New World army ants. Colonies of *Dorylus wilverthi* in the Old World and *Eciton burchelli* in the New World retrieve almost identical sizes of prey item and the overall size range of their workers is very similar. However, 98% of *D. wilverthi* workers are within the size range of the smallest 25% of *E. burchelli* workers. In *E. burchelli* larger workers specialize in prey retrieval, whereas in *D. wilverthi* workers form many more teams than in *E. burchelli*. Such teams compensate for the relative rarity of larger workers in *Dorylus*. The proportions of prey items retrieved by teams in *Dorylus* and *Eciton* are 39% and 5%, respectively. The percentages of all prey biomass retrieved by teams in *Dorylus* and *Eciton* are 64% and 13%, respectively. Working either as single porters or teams, *Dorylus* carry more per unit ant weight than do *Eciton*, but *Eciton* are swifter. However, these different ergonomic factors counterbalance one another, so that performance at the colony level is remarkably, although by no means completely, similar between the Old and New World species. The remaining differences are attributable to adaptations in worker and colony tempo associated with the recovery dynamics of their prey populations. Our comparative analysis provides a unique perspective on worker-level and colony-level adaptations and is a special test of the theory of worker caste distributions.

Keywords: ants; army ants; caste; convergent evolution; *Dorylus*; *Eciton*

1. INTRODUCTION

Convergent evolution provides exceptionally strong evidence of the power of natural selection in shaping adaptations (Darwin 1859; Wilson 1975; Skelton 1993). Dissimilar lineages can produce organisms with striking similarities in form and function when they evolve under similar selection pressures (Hollar & Springer 1997; Moore & Wilmer 1997). Social insects have furnished key tests for many aspects of evolutionary theory (Franks 1990; Hölldobler & Wilson 1990; Bourke & Franks 1995), in part because they exhibit adaptations at both the colony and individual levels and facilitate quantitative analyses of the relationship between the parts and the whole. However, this advantage has rather rarely been used in detailed comparative studies (but see Brown & Wilson 1959; Seeley *et al.* 1982; Gronenberg 1996; Muller 1996; Mueller *et al.* 1998) particularly in studies testing theories about caste distributions (Oster & Wilson 1978).

Massively populous colonies of army ants, *Eciton* in the New World and *Dorylus* in the Old World, have evolved independently (Bolton 1990; Gotwald 1995; Brady 1998) and they are one of the most striking examples of convergent evolution among all social insects (Hölldobler & Wilson 1990; Gotwald 1995). For example, colonies of certain *Eciton* and *Dorylus* species

stage huge swarm raids and both retrieve tens of thousands of fragments of arthropod prey per raid per day over distances of up to approximately 200 m (Franks 1989; Gotwald 1995). Such colossal road haulage has selected for extraordinary allometries of prey carriage in *Eciton burchelli* (Franks 1986). For example, workers form teams and heavier teams can carry disproportionately heavy prey items. Such teams are superefficient: their performance is more than the sum of their parts. A team can carry an item that is so heavy that, no matter how the item was fragmented, the initial members of the team would be unable to carry away all of the fragments. Indeed, when presented with a prey item originally carried by a team, *E. burchelli* workers never fragment such an item but replace the original team with one of almost exactly the same combined weight (Franks 1986).

In Africa, various species of *Dorylus* occupy a similar niche to the one used by *E. burchelli* in Central and South America (Gotwald 1995). For example, *Dorylus wilverthi* also stages huge swarm raids through tropical rainforest, capturing, fragmenting and retrieving a huge diversity of arthropod prey. Here for the first time, to our knowledge, we quantify the prey retrieval performance of single porters and teams of porters of *D. wilverthi*. This facilitates a comparative analysis which reveals some remarkable similarities and differences at the level of individual porters and teams of porters between New and Old World army ants.

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Figure 1. The relationships between prey item dry weight and the dry weight of the ant or ants that were carrying that item for single porters (filled triangles) and teams of porters (open triangles) in *D. wilverthi*, and for single porters (solid circles) and teams of porters (open circles) in *E. burchelli*. The relationship for single porters in *D. wilverthi* can be described by $P = 0.5294S^{1.17}$, where P is the prey item dry weight in milligrams and S is the single porter dry weight in milligrams ($r^2 = 0.58$, $n = 123$, $p < 0.001$ and s.d. of the slope = 0.09). The relationship for teams of porters in *D. wilverthi* can be described by $P = 0.8253T^{1.01}$, where P is the prey item dry weight in milligrams and T is the total team dry weight in milligrams ($r^2 = 0.44$, $n = 100$, $p < 0.001$ and s.d. of the slope = 0.11). The relationship for both sets of *Dorylus* data combined can be described by $P = 0.5710W^{1.18}$, where P is the prey item dry weight in milligrams and W is the porter or total team dry weight in milligrams ($r^2 = 0.59$, $n = 223$, $p < 0.001$ and s.d. of the slope = 0.07). The relationship for single porters in *E. burchelli* can be described by $P = 0.1153S^{1.63}$, where P is the prey item dry weight in milligrams and S is the single porter dry weight in milligrams ($r^2 = 0.52$, $n = 206$, $p < 0.001$ and s.d. of the slope = 0.11). The relationship for teams of porters in *E. burchelli* can be described by $P = 0.1959T^{1.38}$, where P is the prey item dry weight in milligrams and T is the total team dry weight in milligrams ($r^2 = 0.37$, $n = 106$, $p < 0.001$ and s.d. of the slope = 0.17). The relationship for both sets of *Eciton* data combined can be described by $P = 0.1212W^{1.61}$, where P is the prey item dry weight in milligrams and W is the porter or total team dry weight in milligrams ($r^2 = 0.62$, $n = 312$, $p < 0.001$ and s.d. of the slope = 0.07). (*Eciton* data originally published in Franks (1986).) In the 'stack' of four regression lines in this figure the uppermost line is for *Dorylus* teams, then in descending order are lines for *Dorylus* single porters, *Eciton* teams and *Eciton* single porters. The gradients of the regression lines for single porters and teams of porters in *Eciton* are not significantly different from one another ($d = 1.20$ and $p > 0.1$). The gradients of the regression lines for single porters and teams of porters in *Dorylus* are not significantly different from one another ($d = 1.09$ and $p > 0.1$). The gradient of the regression line (not depicted) for all of the *Dorylus* data is significantly less than the gradient of the regression line (not depicted) for all of the *Eciton* data ($d = 4.25$ and $p < 0.001$). Nevertheless, the gradient of the regression line (not depicted) for all of the *Dorylus* data is significantly greater than 1 ($t = 2.52$ and $p < 0.02$).

2. METHODS, RESULTS AND DISCUSSION

Prey transport in *D. wilverthi* was studied in Kibale Forest, Uganda, in July and August 1998, using methods almost identical to those used on *E. burchelli* in Panama (Franks 1986; see also Franks 1985). Figure 1 shows the

relationship between prey item dry weight and the dry weight of the individual ant or team of ants carrying such items for both *D. wilverthi* and *E. burchelli*. In each species heavier workers carry disproportionately heavy items and (heavier) teams of workers carry disproportionately heavy items. In each species there is an almost seamless

extrapolation of performance between single porters and teams of porters. The gradient of the regression line for *D. wilverthi* teams is a close approximation to 1, but the higher intercept for teams than for single porters in this species is such that workers acting as a team can carry more than the sum of their individual performances. Indeed, the regression line through all of these *Dorylus* data combined has a slope significantly greater than 1. Hence, *Dorylus* teams are superefficient.

All army ants carry items by first straddling them so that the item is slung beneath their bodies and, hence, they can cooperate more effectively. By straddling a prey item, two or more army ants can carry the same item slung beneath both of their bodies. In this way, members of a team can and always do face and work in the same direction. By contrast, other ants tend to pull at larger items and several ants often pull in different directions. Furthermore, teams can be highly efficient because rotational forces associated with moving large and cumbersome objects tend to disappear. For example, two people carrying a third between them on a stretcher may well do much less than half the work each would do if they tried to carry a person unaided (Franks 1986). Indeed, as predicted from work on *Eciton* (Franks 1986), when prey items originally carried by teams were returned to the foraging columns of *D. wilverthi* they were never fragmented but carried whole by a new team or, rarely, by a single very large worker.

In *E. burchelli* new teams have an almost identical weight to the team they replace (Franks 1986). In *D. wilverthi*, however, the relationship between the dry weight of the replacements (T_r) and the original teams (T_o) is best described by the equation $T_r = 0.78 T_o$ ($p < 0.001$). Thus, in *D. wilverthi* each replacement team typically weighs only 80% of the original. This may be because different worker castes are available in a foraging column compared to the swarm front from which the prey item was originally retrieved and because our experimental sampling sites were bare, hard-packed soil where lighter groups of ants could work just as well as heavier ones.

Figure 2 shows that the overall range of individual weights of workers is extremely similar in *E. burchelli* and *D. wilverthi*. The median dry weight of workers in *D. wilverthi* (0.49 mg) is, however, less than one-quarter of that of *E. burchelli* (2.30 mg; Franks 1986). Indeed, 98% of *D. wilverthi* workers are within the size range of the smallest 25% of *E. burchelli* workers. Figure 1 shows that the total range of weights of prey items retrieved by single porters or teams of porters is very similar in *E. burchelli* and *D. wilverthi*. Consequently, because the median weight of *Dorylus* workers is much less than that of *Eciton* workers, we predicted that *Dorylus* should form many more teams to compensate both for having smaller workers and relatively fewer larger workers. This prediction was tested and verified by independent, non-intrusive viewing of foraging columns of *Dorylus* colonies. *D. wilverthi* columns were monitored for 50 separate periods of 4 min each, in which a total of 5318 prey items were observed. In *D. wilverthi* 39% of all prey items are retrieved by teams whereas in *E. burchelli* only 5% of prey items are retrieved by teams (Franks 1986). Notice also that in figure 1 the overlap between the performance of single porters and

Figure 2. Frequency/dry weight (mg) boxplots for a large sample of *D. wilverthi* workers taken from a raid column ($n = 1754$) and for a sample of *E. burchelli* workers ($n = 572$; *Eciton* data originally published in Franks (1985)). The *Dorylus* data presented in this figure are from a different sample to those presented in figure 1. The width of each boxplot is proportional to the sample size, the box encompasses the interquartile range, the line across the box is the median, whiskers are drawn to the nearest value within 1.5 times the interquartile range and all remaining outlying points are marked with squares.

teams of porters (as indicated by the overlap in the respective regression lines) is greater in *Dorylus* than in *Eciton*. This is also as predicted given that, over a much larger size range, relatively large workers are much rarer in *Dorylus* than in *Eciton* (figure 2).

The fundamental trade-off here is between more small workers (*Dorylus*) or fewer larger ones (*Eciton*). However, there is another difference. In *E. burchelli* four modes can be recognized in the worker-size frequency distribution (see Franks 1985), whereas in *Dorylus* there is a single mode and a long, smoothly tapering right skew (figure 2). This contrast illustrates theoretical principles first elucidated by Oster & Wilson (1978). The 'manufacturing costs' of producing larger workers will probably rise disproportionately quickly and, hence, populations of specialized large workers (and multimodal worker distributions) are only expected when larger workers are extremely efficient. The submajors and majors in *E. burchelli* exhibit such high individual efficiency. The former are a specialist porter caste and the latter provide a unique defensive capability. The submajors in *E. burchelli* constitute only 3% of the colony's workforce but are 26% of all of the porters of prey. They can shuttle quickly between the nest and the swarm front to collect more prey because, when unburdened, they can run exceptionally quickly. They can retrieve disproportionately heavy items and, when they do so, they run at the same speed as the other porters of prey (Franks 1985, 1986). The majors in *E. burchelli* use their huge specialized mandibles to bite through and remain locked into the flesh of would-be predators (Franks 1985). In this way, they can continue to

sting their adversary in situations in which smaller workers could be easily brushed away.

In the absence of such exceptional individual performance, Oster & Wilson (1978) predicted that the number of physical castes seen will be many fewer than the number of tasks present. The absence of modal groups of larger workers in *Dorylus* fits Oster & Wilson's (1978) prediction precisely, because their role has been filled by superefficient teams of smaller workers. Superefficient teams in *Dorylus* are, in part, surrogates for the submajors in *E. burchelli* (Franks 1985, 1986). This explains why the worker size distribution in *Dorylus* has a single dominant mode among the smaller workers. Thus, the comparison of *Dorylus* and *Eciton* presented here supports the caste distribution predictions of Oster & Wilson (1978). Why *E. burchelli* has submajors rather than just teams of smaller workers will be considered later in this paper.

The gradient of the allometric relationship between prey item weight and the weight of the porter or team of porters is steeper for *E. burchelli* than for *D. wilverthi* (figure 1). However, the intercepts for such relationships are higher for *D. wilverthi* than for *E. burchelli* (figure 1). Hence, weight for weight and across much the same range of weights, *D. wilverthi* individuals or teams carry more than *E. burchelli* individuals or teams.

All else being equal, *D. wilverthi* and *E. burchelli* workers might be expected to be doing similar amounts of work. Hence, the observation that the Old World army ants are carrying more per unit porter weight leads to the prediction that they will be moving more slowly. This second prediction has been verified. Within each species the velocities of individual porters of prey and teams of porters of prey are almost identical. This should minimize traffic congestion (Franks 1986). In *D. wilverthi*, both single porters and teams of porters have an average velocity of 0.03 m s^{-1} (s.d. = 0.004 m s^{-1} and $n=60$ for single porters and s.d. = 0.005 m s^{-1} and $n=50$ for teams). *E. burchelli* velocities, at 0.08 m s^{-1} for both single porters and teams of porters (Franks 1986), are more than twice those of *D. wilverthi*. The median dry weights of prey items carried by *D. wilverthi* single porters and teams of porters are, respectively, 1.323 and 3.713 mg. The comparable data for *E. burchelli* for the median dry weight of prey items carried by single porters and teams of porters are, respectively, 1.115 and 3.310 mg. Considering that 39% of prey items are retrieved by teams in *D. wilverthi* compared with only 5% in *E. burchelli*, the median weight of prey items in such *D. wilverthi* foraging columns is approximately 2.25 mg compared with 1.22 mg in *E. burchelli*. Teamwork makes a major contribution to the foraging effort of these *Dorylus* colonies, with 64% of all of their prey biomass being recovered by teams compared to approximately 13% in *E. burchelli*. This is the first evidence that superefficient teams make an important contribution to total foraging activities in any other species than *E. burchelli* (Franks 1986).

It has been shown that superefficient teams can occur in *Novomessor cockerelli* (Hölldobler *et al.* 1978) and in *Pheidolegeton diversus* (Moffett 1987, 1988). However, in neither of these cases is it known what fraction of all the prey biomass is retrieved by teams in natural unmanipulated conditions. A large proportion of the prey of *Formica*

schaufussi is retrieved by groups which, although they are not biomechanically superefficient, serve to remove large prey items safely to the nest before they can be discovered by competitors (Traniello & Beshers 1991). Group retrieval of prey has also been examined in *Pheidole pallidula* (Detrain 1990; Detrain & Deneubourg 1997), but in this species it is also not superefficient.

Taking both weights and velocities into account, overall *D. wilverthi* porters carry 0.068 mg dry weight of prey per metre per second compared to $0.098 \text{ mg m}^{-1} \text{ s}^{-1}$ in *E. burchelli*. Thus, the proportionately greater weight carried by *D. wilverthi* workers is (more than) compensated for by the greater speed of *E. burchelli* workers. However, the smaller average size of workers in *Dorylus* could be associated with other compensatory advantages. Smaller workers are not only less expensive per capita for their colony to produce but, all else being equal, smaller workers can be produced and become productive more quickly and, hence, their populations should grow more rapidly. The fundamental principles of modular growth are applicable to the growth of worker populations (Bourke & Franks 1995).

This is the best example to date of systematic differences in the patterns of investment in worker castes (smaller and cheaper but slower workers in *Dorylus* versus larger and more expensive but faster workers in *Eciton*) in two highly convergent species of ants. *E. burchelli* workers are bigger and operate at a higher tempo (*sensu* Oster & Wilson 1978) than *D. wilverthi* workers (see above). Why should this be the case? First, bigger animals have lower transport costs (in terms of energy used per unit weight transported per unit distance; see Jensen & Holm-Jensen 1980; Schmidt-Nielsen 1984; Franks 1986). Second, the higher tempo in *E. burchelli* is probably associated with the much higher frequency of emigrations in *Eciton* than in *Dorylus*.

E. burchelli colonies have fixed 35-day activity cycles with a distinct nomadic phase in which, for 15 consecutive days, the colony raids only during the hours of daylight and emigrates each night to a new bivouac site (Schneirla 1971). In contrast, *Dorylus* colonies often raid both day and night and emigrations are an order of magnitude less frequent than in *Eciton* (Gotwald 1995). Thus, *Eciton* has much less time in which to raid than does *Dorylus* and its raids proceed at a greater tempo.

Why, however, should *Eciton* colonies have stereotyped activity cycles with periods of incessant nomadism when *Dorylus* do not have fixed patterns of movement and emigrate relatively short distances? The answer, which we propose here for the first time, to our knowledge, may stem from a difference in diet. *Eciton* colonies, with fixed activity cycles, obtain more than half of their food by preying upon other social insect colonies which are slow to recover from such raids (Franks 1982). Therefore, *Eciton* colonies frequently move to new feeding sites and avoid returning too quickly to their earlier foraging sites. Indeed, Britton *et al.* (1996) have shown through mathematical modelling that 'modern' *Eciton* colonies that move to distant foraging sites and, hence, have a low probability of returning to previous ones too soon will out-compete 'hypothetical ancestral' colonies that have shorter nomadic periods and migratory paths. Such low-movement ancestral colonies do less well because they

often return to areas they have depleted too soon. Thus, activity cycles with long nomadic phases, as in *Eciton*, may be an evolutionarily advantageous strategy, in part because their prey are slow to recover (Britton *et al.* 1996). The corollary of this argument is that, if prey were quick to recover, unnecessary migration, with all its attendant costs, should be selected against. Many *Dorylus* colonies forage mostly upon the larval stages of defoliating insects, such as Lepidoptera and Hemiptera, whose populations will probably recover quickly from raids (Gotwald 1995). This explains why these Old World army ants do not have extensive nomadic phases but often remain in the same nest for variable periods of from three to 45 days, move relatively short distances and return surprisingly quickly to their previous foraging and nesting sites (Gotwald 1995). Thus, we can begin to understand patterns of behaviour both at the colony level and at the level of individual workers and comprehend why differences in tempo and worker size distributions may be selected for by differences in prey dynamics.

The type of analysis presented here opens up the possibility of other comparative analyses of convergent evolution in other social insects in which, uniquely, the relationships between performance among variable parts (for example, polymorphic workers) and the strategy of the whole biological organization (the colony) can be quantified so that trade-offs in evolutionary adaptations can be understood much more completely.

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